Biological history of the Mediterranean Sea with reference to the abyssal benthos

by

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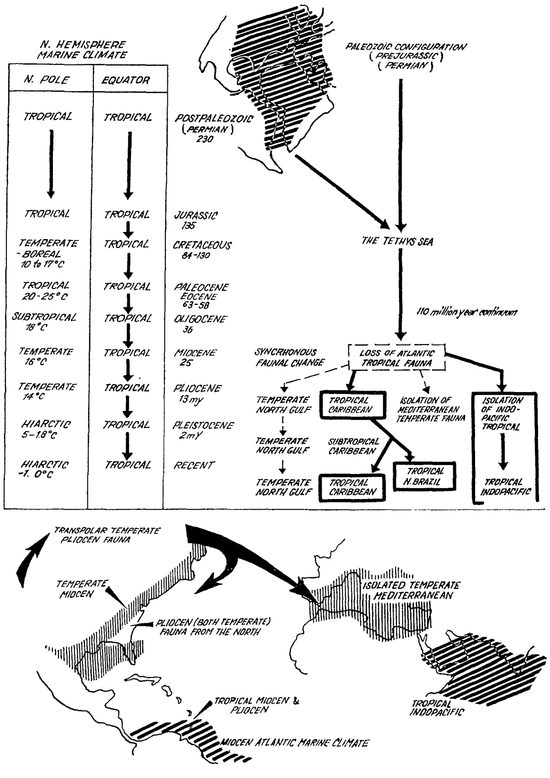
The history of the marine fauna of the world may be understood with considerable clarity through use of the modern geological concepts of sea floor spreading, paleoclimate marine evolution, and continental drift. These three areas of conceptual knowledge provide a rational framework for an understanding of the present composition of the marine fauna on most parts of the earth. There exists the current tendency to provide faunal analysis mainly in terms of glacial and interglacial events. Geologically these events are but a small fraction of the time required for the fauna to reach its present distribution and its present diversity and furthermore the Pleistocene is not marked by the orogenic activity of earlier geological eras when mountains and deep trenches were formed, and epicontinental seas alternately appeared



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and disappeared. The existing biogeographic faunal belts encircling the earth in the Northern Hemisphere, e.g. the Arctic, the boreal, temperate, subtropical and tropical, are in the main Pleistocene events that have been repeated only once before in the Precambrian. The only climates which have existed in an uninterrupted flow in time is the tropical. The boreal, polar, and temperate marine climates are a consequence of glaciation and have appeared and disappeared with glacial times. In the Northern Hemisphere the duration and age of each climate is different with the tropical, the oldest, e.g.

1. Tropical : uninterrupted since the Precambrian, sometimes world wide.
2. Temperate : Oligocene to Recent, in high latitudes and now in midlatitudes.
3. Low Arctic (Boreal) : Pleistocene to Recent, in high latitudes.
4. High Arctic : Pleistocene to Recent, only at the North Pole.

The Mediterranean is located in the Northern Hemisphere and has had a marine climate history peculiar to the Northern Hemisphere with only two Glacial times once during the Precambrian and once the Pleistocene with a remote possibility of some Devonian glaciation. The tropics, and perhaps the subtropics were apparently continuous environments from the Permian onward at least somewhere on earth.

The Indopacific is not a Center of Evolution for Marine Fauna in General or for the Mediterranean in Particular.

The concept of center of evolution as elaborated by FORBES [5] has been used as the starting point for many generalizations that the marine fauna has had a center of evolution and commonly that this center for tropical marine forms has come from the Indopacific.

The evidence for this is based only on the greater number of taxa species, genera, and families which live today in the Indopacific and are either absent today from other regions or represented by fewer comparable taxa. EKMAN [3] saw that this idea was incompatible with the facts of biogeologic history and suggested that the Indopacific was not a center of marine evolution for the tropical fauna and especially for the Mediterranean fauna. Modern concepts of ocean evolution were not available to EKMAN [3] but those concepts which have since been generated and have since revolutionized marine geologic thinking are all in keeping with EKMAN's idea and provide reasonable explanations of the distribution of tropical marine fauna today.

It is now agreed by many, if not most, marine geologists that the American Gulf and Caribbean and the European Mediterranean were once in closer contact physically and in direct contact hydrographically. Their physical separation is believed by BULLARD [1] to have taken place in the Jurassic some 170 millions years ago with the Atlantic ocean being gradually formed as the continents drifted and the Atlantic sea floor deepened. During the Jurassic there existed a world wide tropical sea, the Tethys. During the Cretaceous the Tethys (in the Northern Hemisphere) consisted of a boreal tethys in the region of Norway and New York and a tropical belt of tethys in the lower latitudes extending around the world. By the Eocene the Tethys was still world wide but entirely tropical in marine climate.

The Miocene marks the time in geological history when the marine fauna of the American Gulf of Mexico and Caribbean and the European Mediterranean diverged and each started to take on its special and distinct character. During the Miocene also the Indopacific was fully separated from the Mediterranean by land masses and mountain chains as orogenic activity separated the once continuous tethys into isolated pockets in the American Caribbean and the Indo West Pacific. The Miocene also marks the time of massive extinctions of the former luxuriant Tethys fauna in the Atlantic proper, from the Gulf of Mexico and from the Mediterranean. Acknowledged sites of conservation of the former Tethys are the Indo West Pacific, the Brazilian tropics, the American Caribbean tropics or, in other words, the existing stands of reef-building corals and their associated flora and fauna. The Miocene divergence of the Caribbean and Indopacific scleractinian corals is a good example of the impact of Miocene Atlantic changes on the fauna. The data are shown on Table 1. The loss of the Tropical Atlantic elements from the Mediterranean with their persistence or survival in the Indopacific is shown on Table 2 where the decline of the cidaroid (echinoderm) genera is plotted. During the Pliocene tropical elements such as *Clypeaster* and *Diadema* were replaced in the Mediterranean by elements from the North as transpolar migrants such as *Echinus*, *Stronglocentrotus*, and *Sphaerechinus*. Mollusks show a similar pattern of extinction, migration, and replacement.

TABLE I. — Percentage of scleractinian corals in common between the Indopacific and Caribbean at different geologic times as a % of the total Indopacific genera (data courtesy M. William D. PRESTON)

Geologic Age	Per Cent
Triassic	50
Jurassic	60
Cretaceous	71
Paleocene	50
Eocene	65
Oligocene	58
	——— decline of similarity and faunal divergence
Miocene	35
Pliocene	24
Pleistocene	22

TABLE 2. — Decline of the genera of eastern Atlantic cidaroids (Echinodermata) since the jura. (From EKMAN, 1953)

Time	Number	
M. Jur.	193	
U. Jura.	101	
L.K.	68	
M.K.	65	
U.K.	95	
Eoc.	73	
Mioc.	26	
Plio.	3	
SURVIVAL	E. Atlantic	Indopacific
Recent	4	48

Coincident with the extinction of the formerly widespread tropical Atlantic fauna there occurred a general cooling of the oceans and the commencement of glacial conditions in Antarctica (Figure 1). This event is best documented by the cooling of the low latitude deep-sea temperatures as recorded by EMILIANI [4]. At this time the Atlantic was only two-thirds as wide as it is now, was probably shallower, and it can be envisioned that this lesser volume was more seriously affected by the southern cooling than was the much larger Pacific Ocean. Meanwhile there was cooling also in the Northern Hemisphere from the former tropical conditions of the Eocene, and by the Miocene the Arctic regions were subtropical and by the late Miocene and Pliocene they were temperate. During the Pliocene transarctic migrations of temperate species occurred with these originating in the Pacific and replacing the former tethyan tropical fauna of the North Atlantic and as far south as Florida on the Western Atlantic and as far south as the Mediterranean in the Eastern Atlantic.

The Pleistocene marked the start of the ice ages in the Northern Hemisphere and resulted in a cooling of the Arctic to its present hypopsychral status [MENZIES, 7]. The consequence of this was an impoverishment of the former temperate Arctic seas with the extinction of most of the formerly temperate species. The residual fauna now present in the Arctic is characterized by not one endemic genus and all genera are now living today in the Pacific. The species appear to be eurythermal and euryhaline and the diversity of the fauna is less than elsewhere on earth in a major ocean [DUNBAR, 2]. Simultaneously many of the species which entered the Atlantic via the Arctic transmigration died out and only their fossils remain as evidence for their former existence in the North Atlantic. The Pliocene northern migration of temperate into the Atlantic following Miocene cooling is the key event explaining the present composition of the Mediterranean fauna.

Types of Fauna in the Mediterranean

As a consequence of the events cited above, the Mediterranean fauna consists of the following identifiable types with reference to origin and period of origin :

1. Descendants from the former Tethys... genera located in the Eastern Mediterranean and are of tropical nature. This involves few genera. The sturgeon *Acipenser stellatus* and *Huso huso* are believed to be examples and two genera of cidaroids.
2. Pliocene transarctic temperate migrants... around 16 % of the species (echinoderms).
3. Pleistocene interglacial invaders from Tropical African reservoirs... around 15 % of the species.
4. Pleistocene glacial relicts from the north during glacial times... around 41 % of the species in the Mediterranean.
5. Invaders from the Red Sea via the canals... only 6 % of the species.

The Mediterranean and the Gulf of Mexico have had a parallel history with the major difference being in the closer proximity of the Mexican Gulf to tropical fauna in the Caribbean and the more complete interchange of tropical water and its being located at a lower latitude. Thus it is not astonishing to find more northern elements in the Mediterranean than in the Gulf of Mexico and a stronger affinity of the Gulf of Mexico with the tropics. The Mediterranean appears to show a slightly stronger endemism among its species than the Gulf of Mexico, Table 3.

TABLE 3. — Modern faunal relationships of the N.W. Gulf of Mexico and the Mediterranean to more northern fauna, to the tropics and the amount of species endemism

	to North	to Tropics	Endemism
N. W. Gulf of Mexico 396 spp. invertebrates	68-71 %	20 %	12-13 %
Mediterranean	41 %	15-16 %	15-16 %

The Mediterranean Deep Sea Fauna

The Mediterranean deep sea fauna can only have been derived from a shallow water fauna in the same sense that the deep sea fauna of the Pacific and Atlantic has been derived, but the Mediterranean has had little or at least limited connection with the Atlantic in the past and this was all of a shallow water nature in so far as it is known.

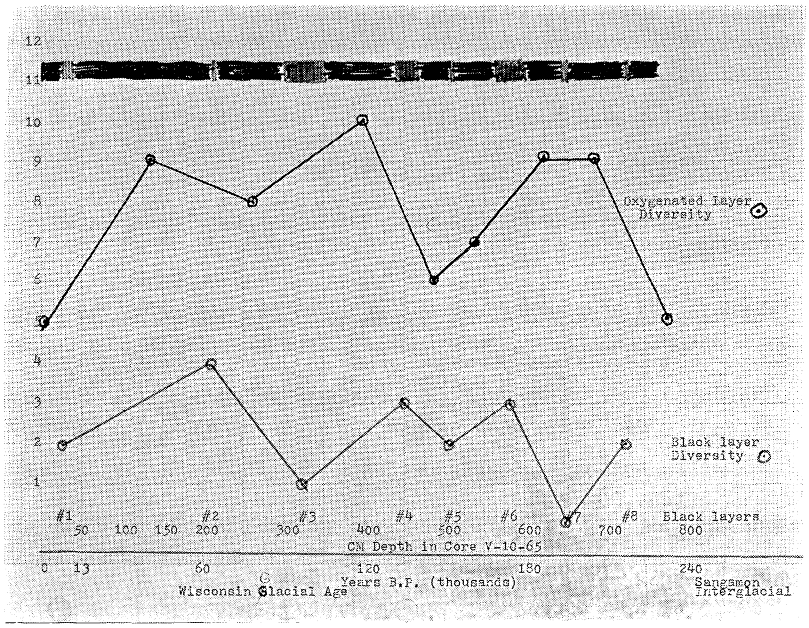

FIGURE 2

Mediterranean Deep Sea Lacks Endemic Genera

The dominant feature of the Mediterranean deep sea fauna is the absence of generic endemism among the genera that live at depths below 2,000 meters. The close connection which exists between the submerged Mediterranean fauna and the deep-sea fauna of the Mediterranean lead Ekman to suggest that the abyssal Mediterranean fauna was an archibenthal abyssal fauna with species from the archibenthal readily entering the deep-sea from shallow water. There is much evidence for this concept. The nearly isothermal 13. degree centigrade water of the Mediterranean is believed to facilitate this penetration of the Mediterranean deeps by the shallow water species.

The marine isopods are in agreement with these suggestions and indicate :

1. The North Atlantic species which enter the Mediterranean are the main pelagic, bathypelagic or shallow water species.

2. Those few benthic and pelagic deep sea species of isopods which exist in the Mediterranean deep sea are mostly endemic to the Mediterranean and are eurybathial below the sill depth at Gibraltar.

3. Not one deep-sea genus of marine isopod is endemic to the Mediterranean deep sea and all of these belong to genera which are world wide in distribution. It is likely therefore that these genera are relict descendents of the tethys sea when it was world wide in distribution.

Not one of these genera is extant today in the Caspian or the Black Sea indicating the different history of those seas as Sarmatic relicts.

Late Pleistocene Changes in the Benthos of the Eastern Basin of the Mediterranean Deep Sea

Since the Pleistocene the deep-sea muds of the Eastern Basin of the Mediterranean and the Red Sea show periodic sapropeltic muds or black layers interspersed with layers of oxidized muds. The black layers have been interpreted as a consequence of anoxic bottom water much like that of the Black Sea and for similar reason; namely that rainfall was excessive and prevented the formation of bottom water [MENZIES, IMBRIE, & HEEZEN, 8]. Since then added study has been made on the benthic faunal remains in the black layers with the resultant conclusions :

1. Black layering of abyssal sediments always resulted in a decline of benthic fauna and an increase in oxidizable remains and inorganic pyrites. For example an average of 181 bone and scale fragments were found in black layers whereas only 19 bones and scales were found in oxidized layers. An average of 8,225 pyrite fragments were found in black layers but only 499 pyrite fragments were found in oxidized layers.

2. Twelve phyla were found as fossil in layers of this core. Seven phyla were never found in black layers. These are Bivalvia (shells), Bryozoa (zoaria), Alcyonaria (spicules), Arthropods (fragments), Holothurians (ossicles), Ophiuroids (vertebrae), and Ostrocods (shells). These groups avoided the black layers.

3. Five groups of organisms were found both in black layers and oxygenated layers, but in a different frequency and abundance.

a. Groups found with a greater frequency and mean abundance in the oxygenated layer are :

Group	Black layer		Oxygenated layer		Statistical Significance
	freq.	mean	freq.	mean	
Foraminifera	0.29	9	0.89	29	+
Echinoids	0.17	3.5	0.7	7.0	+

b. Groups which were either more frequent or of greater mean abundance in black layers are :

Group	Black layer		Oxygenated layer		Statistical Significance
	freq.	mean	freq.	mean	
Barnacles	0.11	0.11	0.05	0.22	0
Worm tubes	0.06	3.0	0.23	1.3	0
Sponge (spicules)	0.8	8	0.5	3.2	0

4. The phyletic diversity in oxygenated layers was always statistically higher than the phyletic diversity of the black layers. This evidence is shown on Figure 2. Testing of this was done using the null hypothesis through an analysis of common variance of the means.

Judging from the analysis of the distribution of benthic fossil remains in a single core (V-10-65, Lamont Geological Observatory) from the deep sea of the Eastern Basin of the Mediterranean and the knowledge that black layers have been correlated throughout the eastern basin by NINKOVITCH & HEEZEN [9] the conclusion is reached that black layers adversely effect the frequency and abundance of the benthos in the deep sea and hence that conditions for life on the bottom were largely unfavorable for benthos periodically in the Eastern Basin of the Mediterranean. Whether conditions equal to those of the Black Sea prevailed and for similar reasons is not known with certainty. Only one black layer (Black layer ≠7) (Figure 2) showed a complete extinction of benthos while others showed a lesser extinction and it seems likely that the degree of hydrographic stratification and anoxia of bottom water was different at different times. Black layer ≠7 is placed at 156,000 years B.P. in the Wisconsin glaciation by extrapolation from the C-14 age data of 7,000 years B.P. for the last black layer.

It is believed that our failure to find benthic isopods in the Mediterranean deeps [MENZIES & GEORGE, 8] may be related to the periodic occurrence of unfavorable conditions for life on the bottom of the Mediterranean during pluvial times in the Pleistocene and we conclude that the Eastern Mediterranean abyssal benthos represents a Pleistocene and Recent event.

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